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Robust retention and transfer of tool construction techniques in chimpanzees

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Abstract

Long-term memory can be critical to a species' survival in environments with seasonal and even longer term cycles of resource availability. The present, longitudinal, study investigated whether complex tool behaviors used to gain an out-of-reach reward, following a hiatus of ca. 3 years and 7 months since initial experiences with a tool use task, were retained and subsequently executed more quickly by experienced than by naïve-chimpanzees. Ten of the 11 retested chimpanzees displayed impressive long-term procedural memory, creating elongated tools using the same methods employed years previously, either combining two tools or extending a single tool. The complex tool behaviors were also transferred to a different task context, showing behavioral flexibility. This represents some of the first evidence for appreciable long-term procedural memory, and improvements in the utility of complex tool manufacture in chimpanzees. Such long-term procedural memory and behavioral flexibility have important implications for the longevity and transmission of behavioral traditions.

Keywords: Memory, tool use, chimpanzee, compound tool.

Multiple memory systems have been identified in various animal species. Caching birds, for instance, have been found to possess impressive spatial memory for hidden foods (Balda & Kamil, 1992; Bednekoff, Balda, Kamil, & Hile, 1997; Kamil & Balda, 1985). Similarly, spatial memory for the presence or absence of out of sight resources has been documented in rats (*Rattus albus*: Olton, Collison, & Werz, 1977) and bees (*Apis mellifera*: Menzel et al., 2005). What, where and when memory, indicative of an episodic-like memory system that stores personal event information, has also been documented in species including scrub jays (*Aphelcoma coerulecens*: Clayton & Dickinson, 1998), hummingbirds (*Selasphorus rufus*: Marshall, Hurly, Sturgeon, Shuker, & Healy, 2013), rats (*Rattus norvegicus*: Babb & Crystal, 2006) and pigeons (*Columbia livia*: Zentall, Clement, Bhatt, & Allen, 2001). Nonhuman animals can also apply retrospective memory to future needs; for example in saving tools (Bonobos: *Pan paniscus* and Orangutans: *Pongo pygmaeus*: Mulcahy & Call, 2006) or storing food in a location they would later visit that would, otherwise, have been devoid of food (Western scrub jays: *Aphelocoma californica*: Raby, Alexis, Dickinson, & Clayton, 2007).

Our closest living relatives, chimpanzees (*Pan troglodytes*), have also been shown to display impressive memory capabilities. Chimpanzees can recall the spatial and ordinal relationship of Arabic numerals presented for milliseconds on a computer monitor (Inoue & Matsuzawa, 2007) and remember what has been hidden and where, for delays of up to around 16 hours (Menzel, 1999). Chimpanzees have also been shown to remember two concurrent and changeable food quantities over a 20 minute period (Beran & Beran, 2004), as well as hidden food locations and food quality following a three month (Mendes & Call, 2014), and ca. 15-30 minute (Sayers & Menzel, 2012) delay, respectively. Chimpanzees have also been found to exhibit improved recall when in possession of task information before exposure to, and opportunity to encode, potential task solutions (Martin-Ordas, Atance, & Call, 2014), as well as improved recognition for items categorically unique among categorically similar items (the ‘isolation effect’: Beran, 2011).

Whilst research has addressed chimpanzees’ ability to retain information following relatively short intervals, little research has addressed whether apes retain information over the course of years. There are, however, notable exceptions. Beran and colleagues (2000) report impressive long-term retention in a symbol-trained chimpanzee, who retained knowledge of lexigrams (geometric patterns used as referents) for 20 years in which she had no access to them. Similarly, Panzee, another lexigram-trained chimpanzee, was able to label objects with corresponding lexigrams despite not having observed the objects for 4 months (Menzel, 1999). Biro and colleagues (2003) also provide anecdotal evidence of impressive long-term memory in a wild chimpanzee. Specifically, one female that migrated to a new group and location where coula nuts were absent appeared to recognize these nuts when they were experimentally provisioned approximately 20 years later. More recently, Janmaat and colleagues (2013) have shown that chimpanzees display goal-directed travel to large fruit trees that carry a high probability of abundant fruit for extended periods, in a manner suggestive of significant long-term “what-where” memory. Specifically, female chimpanzees of the Tai forest, in addition to inspecting trees ‘en route’, locate large trees by goal-directed approach, even when these trees were devoid of fruit and visual/olfactory cues. Such findings suggest that long-term memory of tree locations underpinned a proportion of the foraging trips. Furthermore, tree inspection was predicted by past feeding habits (number of past feeding visits and fruit production) occurring years previously, ultimately suggesting that chimpanzees’ spatial-long-term memory could extend to as long as three years (Janmaat et al., 2013).

Finally, Martin-Ordas and colleagues (2013) recently documented general event memory, whereby chimpanzees and orangutans retained tool use knowledge following a hiatus of 3 years since initial presentation of a tool use task. During the initial tests, subjects were exposed to an experimenter hiding two different tools multiple times in two locations; only one of the tools was functionally appropriate for a subsequent reward-retrieval raking task. During retest, involving presentation of the same experimental apparatus, test area and experimenter, but omitting visual access to the tool hiding event, 10 of 11 experienced subjects searched in the target locations where the tools had been hidden 3 years previously. In general, those that first found the task-appropriate tool, ceased further tool searching behavior, while those who did not, searched the second location (without attempting to use the task-inappropriate tool). This behavior contrasted with that of control subjects without past task knowledge, who failed to search in either tool location (Martin-Ordas et al., 2013).

The study of chimpanzees' long-term memory capabilities after substantial time delays (years) remains in its early infancy and, to date, has been confined to spatial (Janmaat et al., 2013), object/symbol (Beran et al., 2000; Biro et al., 2003) and general event memory (Martin-Ordas, Berntsen, & Call, 2013). Important to the daily activities of many animals is procedural memory, a memory system supporting implicit skill retention, following gradual practice, that does not necessitate memory for past experiences (Gupta & Cohen, 2002). Such procedural memory is thought to subserve 'repetition priming' which describes an enhancement in processing that occurs from past interaction with a particular stimulus, and 'skill learning' describing an enhancement of skill that is not limited to a given stimulus but generalized to other items and tasks (Gupta & Cohen, 2002). Given the complexity of chimpanzee material culture (Sanz, Call, & Morgan, 2009; Whiten, 2011; Whiten et al., 1999) the question of whether procedural memory can support the retention and transfer of complex tool construction/modification behaviors warrants empirical attention. This is especially so given that in the wild seasonally available resources may limit practice opportunities for some tool use behaviors (e.g., seasonally available coula nuts, Tai Forest:

Luncz, Mundry, & Boesch, 2012). Thus, long-term procedural memory may be crucial for the longevity of behavior and transmission of behavioral traditions.

The current study assessed whether chimpanzees retained, and subsequently transferred to a new task, complex tool use behaviors following a hiatus of years in which practice was not possible. Specifically, we retested, following a substantial delay, chimpanzees who, in 2008, had created elongated tools via either of two alternative methods (*combination* of two tools versus *extension* of a single tool) to obtain an out-of-reach reward (Price, Lambeth, Schapiro, & Whiten, 2009). In the earlier study of Price and colleagues of the re-tested chimpanzees, five had witnessed, via video, 'full demonstrations' of a conspecific combining tools and using the manufactured compound tool as a rake, three had witnessed 'partial demonstrations' in which raking was demonstrated with already-combined tools, two received no social information (no video control) and, finally, one was exposed to a video of a conspecific eating a reward in the absence of the task or tools (video control). The present study addressed two important questions: (i) whether chimpanzees, successful at creating an elongated tool to retrieve a reward, would retain their specific method of complex tool manufacture (retention phase) for ca. 3 years and 7 months (test of procedural memory); and (ii) whether chimpanzees transferred tool knowledge to a new task (more general 'skill learning'). To assess whether chimpanzees transferred elongated tool construction we presented a perceptually different transfer task, and, to establish the impact of causal visual feedback of the task's inner mechanisms, used both opaque and transparent forms. To investigate whether the observed tool skills represented simply a proclivity to produce such tool use behavior, we compared the level of, and latency to, success in relation to a control group who had not participated in the original 2008 study. Our ultimate aim was to assess chimpanzee capabilities considered vital to the longevity and transmission of behavioral traditions.

Materials and Methods

Participants

Thirty-one chimpanzees (*M* age = 32 yrs., range 20-48; 12 males), housed at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) in Bastrop, TX USA, participated in this study completed in 2011-12. The KCCMR is fully accredited by the AAALAC-I. Chimpanzees were group housed with access to enriched indoor-outdoor enclosures with climbing facilities. Experienced subjects (*n* = 11) were selected for the current study using the criterion that they created an elongated tool to retrieve an out of out-of-reach reward in 2008 using the combine or extension method (Price et al., 2009). Those that created an elongated tool in 2008 but failed to retrieve a reward with it were not retested. In the original study all of our re-tested chimpanzees, except one, received 17 possible trials, 9 of which required the manufacture of an elongated tool to obtain an out-of-reach reward and 8 of which could be reached with an unmodified tool. One of the re-tested subjects received one trial only, requiring elongated tool manufacture, due to a lack of participation in subsequent trials. Subjects did not gain further experimental or enrichment experience with creating elongated tools between 2008 and 2011/2. Twenty task-naive chimpanzees, selected as they had no prior experience of extending or combining tools to fetch out-of-reach rewards, provided the baseline data; termed ‘control’ or ‘naïve’ subjects according to their participation in the current study (Table 1). No food or water deprivation occurred. Subjects progressed from a retention phase to a transfer phase, which incorporated a) transfer-opaque, then b) transfer-transparent, tasks. Comparisons were made between subjects who had differing levels of experience with the retention and transfer tasks (see Table 1).

[insert Table 1 around here]

Retention Phase

Materials

The raking platform was the same platform originally used by Price and colleagues (2009). The platform was constructed out of acrylonitrile-butadiene-styrene (50 cm x 55) and attached to a wheeled cart (122 cm L x 31 H x 74 W). Grapes were placed either close to (13 cm from the platform edge), or distant from (49 cm from the platform edge, against a 13 cm high wall), subjects. As in 2008, two available tool elements could be ‘combined’ (Table 1) through insertion of a 28 cm rod into the opening of a second tool component (a 39 cm long hollow polycarbonate tube). An alternative tool ‘extension’ method (Table 1) involved twisting and pulling a nylon rod that protruded 3 cm out of the hollow polycarbonate tube. ‘Close’ grapes could be accessed with a single, unmodified tool, while ‘distant’ grape retrieval required an elongated tool. The familiar stimuli presented in the retention phase consisted exclusively of the platform and tools used in 2008. The experimenter who ran all trials and study phases (retention/transfer-opaque/transfer-transparent) in 2011/12 was not the experimenter who ran the original study in 2008. Trials were recorded on a Sony Handycam DCR-SR58E (see online resources 1-3 for example videos).

Procedure

Subjects were tested individually and voluntarily in their indoor compartments (ca. 2.4 m x 2.4 x 1.8). The raking platform was positioned in front of the subject, flush against the enclosure mesh. Test sessions lasted 20 minutes or until all 8 grapes were retrieved (4 close and 4 distant grape placements, presented in a pseudo-randomized order, such that one distance would not reoccur in succession more than three times, with the location of grape placement on the first trial counterbalanced across subjects). A maximum of three sessions were conducted per subject. Trials began after placement of grapes and tool elements by the experimenter (GV). After each successful grape retrieval, subjects returned the tool elements to the experimenter (who dismantled them), cued by a trained ‘give’ gesture. All subjects voluntarily participated in the procedures and their return for multiple trials suggested that the procedures were enriching/stimulating for them. Following this phase subject’s transfer of tool knowledge was assessed.

Transfer Phases

Materials

The transfer boxes (40.6 cm L x 21.6 H x 30.5 W) presented a task considerably different from that offered by Price et al. (2009) and consisted of either a black or transparent polycarbonate box, on a wheeled cart (59.7 cm L x 63.5 H x 45.7 W), inside which were two mechanisms (close and distant), which when pushed using a tool, would release grapes from a feeder tube positioned on top of the box (see Figure 1). The transparent box enabled visual access to the box’s inner mechanisms (two sliding cuboids, one closer to the subject than the other, each of which would release a reward when pushed with a tool), while the opaque box prevented visual access. In both task variants (transparent or opaque), transparent feeder tubes, one close and one distant from the subject, enabled subjects to see the food rewards. A single, unmodified, tool could be inserted into an opening in the front of the box to release the close mechanism. Note that success required subjects to insert the tool into the centre of the box and not towards the food reward positioned on top of the box, thus presenting a complexity regarding behavioral inhibition (Vlamings, Hare, & Call, 2010). To release the distant mechanism, two tools had to be applied, either through combining them or using a serial method of inserting the smaller of the two tools first, followed by the larger tool. The close mechanism could be released with a combined tool only if subjects inserted the tool into the box center at an angle. Thus, utilizing a combined tool during close trials was inefficient, if not ineffective, contrasting with the raking task. The two tools provided measured 23.2 cm (1.9 cm diameter) and 28.5 cm (2.8 cm diameter) (coloured red and yellow, respectively). Grapes were baited via two transparent feeding tubes attached to the top of the box and, upon release, rolled onto a tray beneath the box. The grapes were visible to chimpanzees in both transfer phases.

[insert Figure 1 around here]

Procedure

All subjects were exposed first to the opaque, and then the transparent, transfer task to initially restrict access to causally relevant information regarding the inner mechanisms of the box. That is, we were interested in whether chimpanzees would transfer a known behavior to a new context without the need for visual access to the box's inner mechanisms (i.e., whether they can rely on procedural memory rather than, new, causal information regarding how the task can be solved). The transparent box then allowed us to assess whether subjects would create elongated tools more flexibly, depending upon need (grape distance), when provided with visual access to how the box works, relative to when this information was restricted. For the transfer-opaque phase, three grapes constituted the reward. Each feeder tube was baited individually depending upon trial type (close or distant). To encourage initial participation, all subjects received a close trial first, followed by a distant trial, with the last 6 trials randomized. In the subsequent transfer-transparent phase, grape quantities were increased (3 for each close, and 15 for each distant, trial) to enhance motivation (trial distances were randomized with first trial distance counterbalanced across subjects). For both transfer studies, a maximum of three 20-minute sessions were conducted, with termination of a session if rewards were retrieved on all 8 trials (4 close and 4 distant).

[insert Table 2 around here]

Video Coding and Statistical Analysis

Video sessions of the retention phase were coded using a scheme closely following Price and colleagues (2009, Table 2). Subjects were assigned tool manipulation scores according to the level of tool manipulation performed, relating to the combine and extension methods (retention: maximum score 14 = successful retrieval with combined or extended tool, minimum score 0 = no tool contact, Table 2). Behaviors recorded during the transfer phases were coded, from video, using a separate coding scheme ((transfer: maximum score 22 = successful combine and grape retrieval (holds yellow tool end of combined tool, inserting red end), minimum score 0 = did not approach the task, Table 3)). For all phases, higher scores represent greater complexity of tool manipulation. Six sessions from each phase were coded by an independent coder, with high coding reliability across tool manufacture ratings (Kappa Coefficients: retention = .93; transfer-opaque = .92; transfer-transparent =

.88). Due to the ordinal nature of the data, and normality violations, non-parametric two-tailed statistical analyses are reported.

[insert Table 3 around here]

Results

Retention Phase

Experienced subjects' (Price et al., 2009) highest tool use scores were predicted by their scores attained in the original study conducted in 2008 (combine index, Spearman rank correlations: r_s = . 74, n = 11, p = .009; extension index: r_s = . 63, n = 11, p = .038; see Table 4 for individual scores across study phases). All the experienced subjects who manufactured an elongated tool in 2008 did so in 2011/12 except for KO. KO failed to progress beyond his first trial which required elongated tool manufacture (distant grape trial) and thus did not retrieve any grapes during the retention phase (Table 5).

[insert Table 4 around here]

Latencies to retrieve a grape using a constructed, combined tool were significantly lower in the retention phase in 2011/12 than in 2008, implying long-term procedural memory rather than tool-use proclivity or tool manufacture rediscovery in these individuals (Wilcoxon signed-rank test: W = .00, n = 7, p = .018, see Figure 2). JI, KT and CL, who were the only three subjects to previously create an elongated tool using the extension method in 2008, did so again in the current study, although KT did so in-between trials prior to returning the tools to the experimenter. An additional female, JE, discovered the extension method (Table 5).

[insert Figure 2 here]

[Insert table 5 here]

Experienced subjects (n = 11) attained higher scores on the combine index (MD = 14.00) than controls (MD = 2.00, Mann-Whitney U test: U = 3.50, n = 21, p < .001, Figure 3). Only one control subject (n = 10), QY, constructed a combined tool, though she failed to retrieve a grape. There was no significant difference in the highest score attained by experienced (MD = 6.00) and control (MD = 4.50) subjects on the extension index pertaining to the twist and pull method of tool elongation (Mann-Whitney U test: U = 44, n = 21, p = .452).

[insert Figure 3 around here]

Overall, experienced subjects achieved high success, with the majority of subjects (n = 8 achieving 100% success, see Table 6) retrieving all eight (4 close and 4 distant) grapes, contrasting with 5 control subjects (of 10) retrieving only close grapes with an unmodified tool (range: 1-3 grapes, see Table 6). Unlike the experienced subjects, no control subject successfully created an elongated tool (by combination or extension) to retrieve a distant grape.

[insert Table 6 around here]

Transfer Studies

Following the retention phase, experienced subjects and controls were exposed to the transfer task, in its opaque and then transparent form. CL (experienced with tool extension) did not voluntarily separate from her group and was thus excluded as a subject for subsequent transfer tests.

Transference of skills to a new causally opaque task? Experienced subjects' scores in the transfer-opaque test were significantly correlated with manipulative performance scores attained in the retention phase (Spearman rank correlation: $r_s = .64$, $n = 10$, $p = .045$). Experienced subjects' latency (seconds) to gain the reward during the first distant trial in the transfer-opaque phase (*MD* = 632) exceeded their latency to first retrieve a grape using a combined tool during the retention phase ((*MD* = 36; Wilcoxon signed-rank test: $W = -2.37$, $n = 7$, $p = .018$; note that latency was not derived from the first close trial with the opaque box as use of a combined tool was inefficient, if not ineffective, contrasting with the raking task. As both close and distant trials in the retention phase could be accessed with a combined tool, latency was measured as time taken to first retrieve a grape with a combined tool (irrespective of reward distance)). Experienced subjects' tool manipulation scores were higher (*MD* = 22.00) than control subjects, one of whom (QY) combined previously in the retention phase (*MD* = 5.00: Mann-Whitney U test: $U = 5.50$, $n = 20$, $p = .001$); they also completed more trials in terms of retrieving grapes (*MD* = 5.50; possible 8 trials) than control subjects (*MD* = .00, Mann-Whitney U test: $U = 7.00$, $n = 20$, $p < .001$, see Table 6). Note that all first trials were close grape placements and thus, as the majority of controls failed to progress from the first trial, the need for combined tools was limited. Only one of the experienced subjects (KO) failed to create an elongated tool. KT created an elongated tool but failed to retrieve a reward with it. KA, KY and JE (experienced subjects) also discovered the serial method (see Table 4).

Investigating transference of skills to a new transparent task. When subsequently presented with the transparent box eight of the 10 experienced subjects combined tools to release grapes from the baited feeder tubes. Of the experienced subjects, KO and KT failed to retrieve rewards using an elongated tool (see Table 6). KO only retrieved one close trial reward with a single tool and KT retrieved no rewards irrespective of trial distance.

AL and MXI (2 of the 10 naïve subjects who had not experienced the opaque box or retention test) and QY (one of the 10 control subjects) successfully combined tools, but failed to release grapes with them. QY used the serial method to gain a reward during one close trial. ZY (control subject) also discovered the serial method but failed to release rewards. MXI, OI (naïve subjects) and ZY (control subject) all released, using a single tool, the reward during a close grape trial.

There was a significant effect of experience on the tool manipulation scores attained (Kruskal-Wallis H test: X^2 (2) = 16.26, $p < .001$) and on the number of reward retrievals (8 trials possible per subject, Kruskal-Wallis H test: X^2 (2) = 19.29, $p < .001$). Post-hoc paired comparisons (Mann-Whitney U tests, Bonferroni adjustment applied $\alpha = .017$) revealed that experienced subjects attained significantly higher tool manipulation scores (*MD* = 22.00) than naïve (*MD* = 8.00; $U = 9.50$, $n = 20$, $p = .001$) and control subjects (*MD* = 3.50; $U = 5.50$, $n = 20$, $p < .001$). Experienced subjects retrieved rewards on significantly more trials (*MD* = 8) than naïve (*MD* = 0.00): $U = 6$, $n = 20$, $p < .001$) or control subjects (*MD* = .00: $U = 7$, $n = 20$, $p < .001$; Bonferroni adjustment applied $\alpha = .017$). There was no significant difference in latency (seconds) to retrieve the grape reward on the first distant trial across transfer phases for 8 experienced subjects (opaque: *MD* = 424; transparent: *MD* = 61; Wilcoxon signed-rank test: $W = -1.40$, $n = 8$, $p = .161$; two chimpanzees, KO and KT, were excluded from the analysis as they failed to retrieve grapes using a combine tool in one, or both, of the transfer phases. JI, whose latency data were missing for the 2008 study, was included in the analysis).

Performance across studies. Experienced combiners retrieved a similar number of rewards across all three phases (retention/transfer-opaque/transfer-transparent; Friedman test: X^2 (2) = 4.52, p = .095). In the Transfer phase, task transparency appeared to influence the number of combined tools created by experienced combiners according to grape distance (N = 226; Chi Square: X^2 (1) = 15.34, p < .001, phi = .26); experienced combiners combined more tools during close (n = 102) than distant (n = 57) trials with the opaque task (Binomial: p < .001), but more combined tools were created during distant (n = 43) than close (n = 24) trials with the transparent task (Binomial: p = .027). No improvement was recorded in the number of rewards retrieved by control subjects across study phases (retention/transfer-opaque/transfer-transparent; Friedman test: X^2 (2) = 2.57, p = .438).

Discussion

Chimpanzees retained the ability, over ca. 3 years and 7 months without practice, to construct elongated tools, to gain otherwise inaccessible rewards. This shows considerable retention of complex tool construction behaviors. Furthermore, those chimpanzees competent at making the tools were able to apply this retained skill to new tools and task situations and did so with appropriate flexibility (using combination more for distant than close grapes) when provided with additional opportunity to practice, and task-relevant visual information (transfer-transparent phase).

Retention of Tool Use Techniques

The majority of chimpanzees persisted with their original method, or methods, of tool creation. Those experienced with the extension method of elongated tool manufacture produced such tools during retest. Similarly, all but one chimpanzee, who previously created combined tools, retained this capability. Such high levels of retention indicate that once a method was mastered, chimpanzees retained this specific capability. Interestingly, three individuals in the present study retained the extension method of tool manufacture after receiving reinforcement in the form of only one (n = 1), or no (n = 2), grapes in 2008. This indicates that, assuming individuals were not re-discovering the extension method, even after one trial learning and minimal or no reinforcement via rewards, procedural memory for complex tool behavior may be retained for extended periods. Independent discovery of tool behaviors was ruled out by the current data, since latencies to retrieve grapes were shorter following, than before, the ca. 3 years and 7 months hiatus. Furthermore, latencies to retrieve rewards using a combined tool were longer when experienced subjects were presented with the less cued novel transfer box (same experimenter as in the retention phase but different tools and task), which required skill transfer, than when they were presented with the retention task. Coupled together, these findings indicate that tool manipulation during the retention phase was supported by participants' long-term procedural memory. Moreover, there was minimal evidence (one control among 10) of asocial learning of tool combining. This subject failed to use the compound tool to retrieve a reward, indicating limited causal understanding of manufactured tool function (Price et al., 2009).

Chimpanzees possess notable memory capabilities (Inoue & Matsuzawa, 2007; Menzel, 1999). Until recently, the long-term memory capabilities of chimpanzees had largely been neglected. The current findings, coupled with those reported by Martin-Ordas and colleagues (2013) are suggestive that, at least for some motor tasks, chimpanzees retain information regarding the tools required for a task and how to construct them beyond three years. Future research could consider extending test and re-test hiatuses to longer periods. In particular, as chimpanzee recognise specific resources and symbolic referents for up to 20 years (Beran et al., 2000; Biro et al., 2003), it would be of interest to examine whether procedural knowledge is retained following similar hiatuses.

Such long-term procedural knowledge is perhaps unsurprising given the longevity of certain food extraction traditions for foods that can be infrequently available in the wild (Mercader et al., 2007). For example, the practice of cracking nuts, some of which are edible only certain months of the year (Luncz et al., 2012), requires the long-term retention of precise percussive motor actions and appropriate tool materials to serve as hammers and anvils. Previous studies have suggested that chimpanzees are capable of retaining resource locations, as well as functionally appropriate tools for a known task, for periods of around 3 years (Janmaat et al., 2013; Martin-Ordas et al., 2013). The current study adds to these findings showing that chimpanzees retained significant procedural memory concerning tool creation. Coupled together these studies suggest that chimpanzees long-term memory can retain ‘where’ (Janmaat et al., 2013; Martin-Ordas et al., 2013), ‘what’ (Martin-Ordas et al., 2013), and ‘how’ (current study) information for at least ca. 3 years.

Transfer of Tool Use

Our secondary aim was to (i) establish whether chimpanzees would transfer tool knowledge to a new task situation, and (ii) evaluate the impact of visual causal information on levels of tool combining. Variants of the trap-tube experiment (Visalberghi & Limongelli, 1994), in which animals must retrieve a reward by avoiding a trap, reveal that animals, including chimpanzees, can experience difficulty in transferring past task knowledge even to perceptually similar tasks (Martin-Ordas, Call, & Colmenares, 2008; Seed, Tebbich, Emery, & Clayton, 2006). However, our results indicated that the majority of experienced subjects were able to combine novel tools to solve a perceptually novel task. This contrasts with subjects who, despite exposure to the raking task (controls) or no such exposure (naïve subjects), failed to combine tools to release out-of-reach rewards. This suggests that chimpanzees' procedural memory enhanced performance with new stimuli. That is, exposure to, and success with, the retention stimuli enabled skill transferral to novel stimuli. Future studies could assess whether chimpanzees engage in 'skill learning' which requires enhanced performance resulting from multiple exposures to novel stimuli (Gupta & Cohen, 2002). This could be assessed by presenting subjects with multiple novel tool components that can be combined to make a single compound tool. Finding that experienced subjects' performance with novel stimuli was enhanced due to exposure to past, but different, stimuli, relative to naive subjects, is nevertheless an important first step to testing whether chimpanzee's procedural memory supports skill transfer. Such skill transferral in the wild would be valuable for animals facing new, or changing, environments where similar problems may be encountered.

Experienced subjects were markedly persistent in their attempts to use combined tools, creating 102 combined tools, for close grape trials that were reachable with a single, unmodified tool in the Transfer-Opaque phase, despite high levels of unsuccessful attempts (see also Hrubesch, Preuschoft, & van Schaik, 2009). Note that close grapes could readily be retrieved with a combined tool in the retention phase whereas in the transfer phases close grape reward retrieval with a combined tool was more difficult. Rather than suggesting a breakdown in the flexibility of elongated tool manufacture depending upon need, it is likely that the restricted task-relevant visual information in this condition limited understanding. By contrast, flexible action appropriate to context was enhanced, creating comparably fewer combined tools during close grape trials (n = 24), with the transparent task in which subjects could see two internal mechanisms, one closer to the subject than the other, which could be pushed to release the rewards. Due to the order of opaque-then-transparent task presentation, it is difficult to ascertain whether this improvement was due to practice effects or newly acquired causal information. Our result is, however, reminiscent of chimpanzees disregarding observed task-irrelevant actions (modelled actions that serve no function in relation to obtaining the task goal) in their copying of techniques when applied to transparent, rather than opaque, task boxes, the former of which revealed relevant causal information (Horner & Whiten, 2005).

The degree to which causal reasoning, trial and error learning, insight or response transfer to similar stimuli, underpin complex tool use, remains contentious (Hihara, Obayashi, Tanaka, & Iriki, 2003). Regarding obtaining out-of-reach rewards using tools, it appears that prior experience of creating a compound tool was beneficial in enabling chimpanzees to create and use a similar tool to access rewards from a different task, as indicated by experienced subjects outperforming control subjects in the transfer phases. For serial tool use (possible with the transfer task), our results suggest that transfer from prior experience was not essential, as one control subject (QY), without combining experience, used this method to gain grapes during the transfer test. It is perhaps most parsimonious to consider that serial tool use occurred through iterated behavior; that is, upon one tool insertion not releasing the grapes, this action was repeated by inserting a second tool.

In sum, chimpanzees displayed proficient complex tool use, retaining specific methods of tool manufacture over more than 3 years, and transferring these skills to a new context with efficiency (generally flexible tool construction according to reward distance: transfer-transparent phase). The retention of complex tool behavior, despite an interim absence of raw materials to manufacture tools or resources requiring their use, is important for the long-term maintenance of behavioral variants preventing repertoire loss. Similarly, transferring skills to new contexts will allow behavioural flexibility and adaptation to new or changing environments (Boesch, 1995). Such memory capabilities and behavioural flexibility are, along with social learning, key components that enable the accumulation of cultural traits and, in humans, the progressive ratcheting of cultural complexity (Dean, Vale, Laland, Flynn, & Kendal, 2014).

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Figure 1. (i) Transfer-opaque task; (ii) Transfer-transparent task

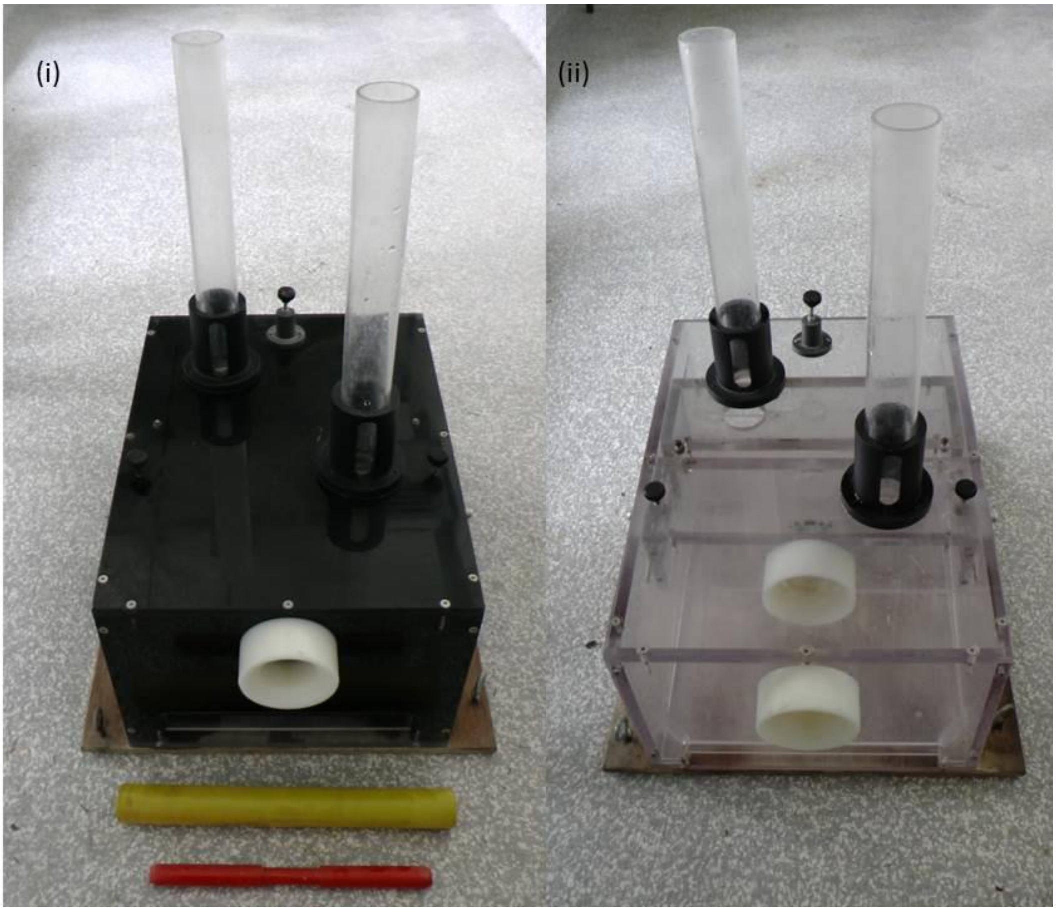

Figure 2. Latencies to first retrieve a grape using a constructed, combined, tool in Price et al. (2008) and in the retention phase. Note: KO who failed to construct a combined tool in 2011/12, JE due to lack of task participation during the 1st two 20-minute sessions, and JI due to mislaid original data file from 2008, were excluded from the analysis.

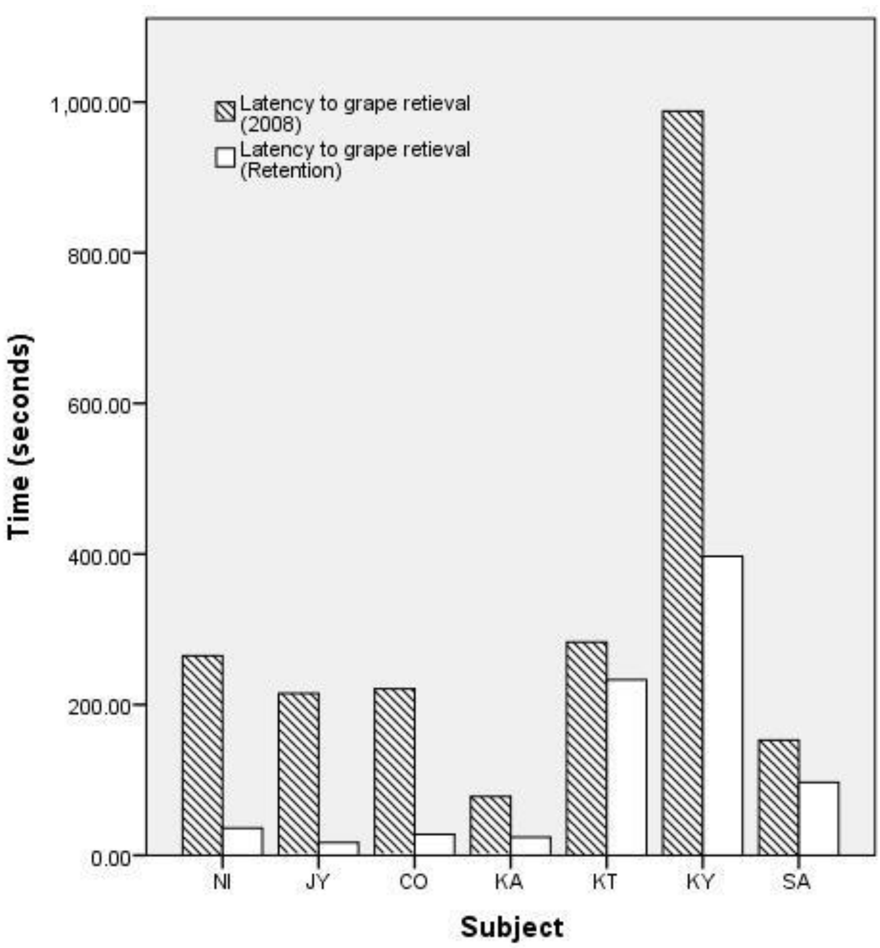

Figure 3. Median tool manipulation scores (black horizontal line) and interquartile ranges (boxes) according to study phase and participant experience. Whiskers represent the minimum and maximum manipulative performance scores (unclassified outliers represented by circles or extreme cases by asterisks). Note that all but two experienced subjects achieve the maximum score of 14 in the retention phase. Scores relate to the combine index for the retention phase.

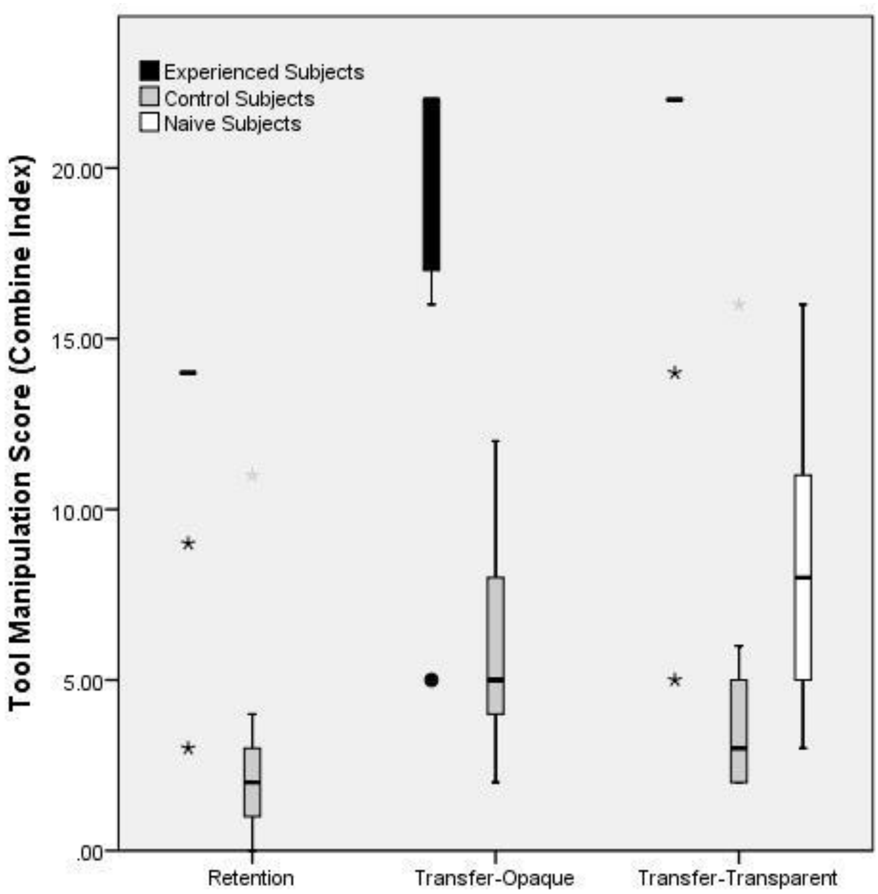

Table 1.

Chimpanzee Participation in the Study's Phases and Terminology

		Study Participation			
Terms	**Description**	**Price et al. Study**	**Retention Phase**	**Transfer-Opaque Phase**	**Transfer-Transparent Phase**
Experienced Subjects	Created an elongated tool to retrieve a grape in 2008 by combining or extending tools (*N* =11).	✓	✓	✓	✓
Control Subjects	Baseline for experienced subjects (*N* =10)	✓	✓	✓	✓
Naïve Subjects	Baseline for the Transfer-Transparent phase only (*N* =10)	×	×	×	✓

		Method Availability			
Term	**Description**	**Price et al. Study**	**Retention Phase**	**Transfer-Opaque Phase**	**Transfer-Transparent Phase**
Combine Method	Creation of an elongated tool by insertion of one tool into the end of a second tool	✓	✓	✓	✓
Extension Method	Creation of an elongated tool by pulling an internal rod from a single tool (twist and pull action)	✓	✓	×	×
Serial Method	Successive insertion of two unconnected tools into the transfer boxes	×	×	✓	✓

Table 2.

Combine and Alternative Tool Manipulation Scores based on 'Price et al (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society Series B; Biological Sciences*, 276(1671), 3377-3383.'

Combine Index	Score	Extension Index
Successful retrieval with the combined tool	14	Successful retrieval with the extension method
Combine tools successfully, retrieval attempt with combined tool	13	Successful modification (twist and extend), retrieval attempt with modified tool
Combine tools successfully, retrieval or retrieval attempt with either or both unmodified components	12	Successful modification, retrieval or retrieval attempt with either or both unmodified tools
Combine tools successfully, no retrieval attempt	11	Successful modification, no retrieval attempt
Combine attempt with hollow (correct) end, retrieval or retrieval attempt with either or both unmodified components	10	Twist and pull attempt (unsuccessful modification), retrieval or retrieval attempt with either or both unmodified components
Combine attempt with hollow end, no retrieval attempt	9	Twist and pull attempts, no retrieval attempt
Combine attempt with black (incorrect) end, retrieval or retrieval attempt with either or both unmodified components	8	Twist attempt, retrieval or retrieval attempt with either or both unmodified components
Combine attempt with black end, no retrieval attempt	7	Twist attempts, no retrieval attempt
Insert finger into hollow end, retrieval or retrieval attempt with either or both unmodified components	6	Pull attempt, retrieval or retrieval attempt with either or both unmodified components
Insert finger into hollow end, no retrieval attempt	5	Pull attempts, no retrieval attempt
Look into or mouth hollow end, retrieval or retrieval attempt with either or both unmodified components	4	Bite or hand touch to black end, retrieval or retrieval attempt with either or both unmodified components
Look into or mouth hollow end, no retrieval attempt	3	Bite or hand touch to black end, no retrieval attempt
Retrieval or retrieval attempt with either or both unmodified components	2	Retrieval or retrieval attempt with either or both unmodified components
Contact, but no retrieval attempt	1	Contact, but no retrieval attempt
No contact	0	No contact

Table 3.

Tool Manipulation Scores for Transfer Phases (Opaque and Transparent)

Tool Manipulation Score (Descriptor)	Code
Successful combine and retrieves grapes (holds yellow tool end of combined tool, inserting red end)	22
Successful combine and (close) and retrieve grapes (holds red tool end of combined tool, inserting yellow end)	21
Successful combine, retrieval attempt by inserting red tool end and holding yellow end	20
Successful combine, retrieval attempt by inserting yellow end of tool first	19
Successful combine of yellow and red tool components preceding tool deconstruction, and retrieve grapes with either unmodified tool	18
Successful combine preceding tool deconstruction, retrieval attempt with unmodified tool	17
Successful combine, no grape attempt	16
Serial method to retrieve grapes (one tool is inserted before the other, essentially combining the tools once one is inside the box)	15
Serial method and retrieval attempt	14
Attempt to combine but tools do not insert correctly to combine into a single tool, followed by close grape retrieval with unmodified tool	13
Attempt to combine and retrieval attempt	12
Attempt to combine, no grape attempt	11
Insert finger into hollow end of yellow tool and retrieve grapes with the tool	10
Insert finger into hollow end of yellow tool and retrieval attempt	9
Insert finger into hollow end of yellow tool and no grape attempt	8
Look or mouth hollow end of yellow tool before retrieving grapes with the mouthed/looked at tool	7
Look or mouth hollow end of yellow tool before retrieval attempt with the tool	6
Look or mouth hollow end of yellow tool and no grape attempt	5
Successful retrieval of grapes with single tool	4
Grape attempt with one tool	3
Contact but no attempt	2

No contact	1
No task approach	0

Table 4.

Chimpanzee's highest attained Tool Manipulation Scores according to Study Phase

			2008		Retention		Transfer-Opaque		Transfer-Transparent	
Participant	**Experience**	**Social information seen in 2008**	**Combine Index Score**	**Extension Index Score**	**Combine Index Score**	**Extension Index Score**	**Tool Manipulation Score**	**No. of reward retrievals using the Serial method**	**Tool Manipulation Score**	**No. of reward retrievals using the Serial method**
NI	Experienced	Combine	**14**	6	**14**	2	**22**	0	**22**	1
JY	Experienced	Combine	**14**	2	**14**	0	**22**	0	**22**	0
KO	Experienced	Combine	**14**	6	9	6	5	0	14	0
CO	Experienced	Combine	**14**	3	**14**	3	**22**	0	**22**	0
KA	Experienced	Combine	**14**	4	**14**	8	**16**	2	**22**	2
KT	Experienced	Partial	**14**	**12**	**14**	3(**14**)	**17**	0	5	0
KY	Experienced	Partial	**14**	6	**14**	3	**22**	3	**22**	5
SA	Experienced	Partial	**14**	10	**14**	10	**22**	0	**22**	0
JE	Experienced	Video Control	**14**	6	**14**	**11**	**22**	1	**22**	0
JI	Experienced	No Video	**14**	**12**	**14**	**14**	**22**	0	**22**	0
CL	Experienced	No Video	10	**14**	3	**14**	X	X	X	X
KI	Control	NA	X	X	3	5	12	0	5	0
MI	Control	NA	X	X	0	5	5	0	2	0
PI	Control	NA	X	X	1	1	3	0	2	0
PA	Control	NA	X	X	4	3	5	0	5	0
QY	Control	NA	X	X	**11**	7	12	0	**16**	1
SBA	Control	NA	X	X	2	7	5	0	2	0
SY	Control	NA	X	X	1	3	2	0	2	0
SE	Control	NA	X	X	2	2	4	0	2	0
UA	Control	NA	X	X	2	10	8	0	6	0
ZY	Control	NA	X	X	2	4	6	0	14	0
AX	Naïve	NA	X	X	X	X	X	X	8	0
AL	Naïve	NA	X	X	X	X	X	X	**16**	0
BN	Naïve	NA	X	X	X	X	X	X	5	0
DI	Naïve	NA	X	X	X	X	X	X	5	0
HH	Naïve	NA	X	X	X	X	X	X	8	0
MI	Naïve	NA	X	X	X	X	X	X	3	0
MA	Naïve	NA	X	X	X	X	X	X	8	0
MXI	Naïve	NA	X	X	X	X	X	X	**16**	0
OI	Naïve	NA	X	X	X	X	X	X	11	0
PL	Naïve	NA	X	X	X	X	X	X	5	0

Note : For 2008 and Retention fully elongated tool manufacture ≥11 (shown in bold); elongated tool to retrieve grapes = 14. For Transfer phases full combine ≥16 (shown in bold); serial method = 14 & 15.For the social information seen in 2008 'combine' represents subjects exposed to a full video demonstration of a conspecific combining two tools and retrieving a reward; 'partial' represents video exposure to a conspecific retrieving a reward with an already combined tool; 'no video' control represents no video exposure; 'video control' represents exposure to a video of a conspecific consuming a reward. Scores in brackets represent tool manipulation performed between trials.

Table 5.

Type of Tool Manufactured by Experienced Subjects and Success in Retrieving an Out-of-Reach Reward with it in 2008 and 2011/2

	Combined Tool				Elongated Tool (Twist and Pull)			
Experienced Subject	Successful Manufacture (2008)	Reward Retrieval (2008)	Successful Manufacture (2011/2)	Reward Retrieval (2011/2)	Successful Manufacture (2008)	Reward Retrieval (2008)	Successful Manufacture (2011/2)	Reward Retrieval (2011/2)
NI	✓	✓	✓	✓	×	×	×	×
JY	✓	✓	✓	✓	×	×	×	×
KO	✓	✓	×	×	×	×	×	×
CO	✓	✓	✓	✓	×	×	×	×
KA	✓	✓	✓	✓	×	×	×	×
KT	✓	✓	✓	✓	✓	×	✓*	×
KY	✓	✓	✓	✓	×	×	×	×
SA	✓	✓	✓	✓	×	×	×	×
JE	✓	✓	✓	✓	×	×	✓	×
JI	✓	✓	✓	✓	✓	×	✓	✓
CL	×	×	×	×	✓	✓	✓	✓

Note. * indicates tool manufacture occurred between trials

Table 6.

Number of Rewards Retrieved by each Subject across Study Phases according to Grape Distance (out of 4 Close and 4 Distant Trials)

		Retention		Transfer-Opaque		Transfer-Transparent	
Subject	**Experience**	**Successful Close Trials**	**Successful Distant Trials**	**Successful Close Trials**	**Successful Distant Trials**	**Successful Close Trials**	**Successful Distant Trials**
NI	Experienced	4	4	3	1	4	4
JY	Experienced	4	4	3	4	4	4
KO	Experienced	0	0	0	0	1	0
CO	Experienced	4	4	4	4	4	4
KA	Experienced	4	4	2	2	4	4
KT	Experienced	4	4	1	0	0	0
KY	Experienced	4	4	4	4	4	4
SA	Experienced	4	3	2	1	4	4
JE	Experienced	4	4	4	4	4	4
JI	Experienced	4	4	4	4	4	4
CL	Experienced	1	1	-	-	-	-
KI	Control	3	0	0	0	0	0
MI	Control	0	0	0	0	0	0
PI	Control	0	0	0	0	0	0
PA	Control	1	0	0	0	0	0
QY	Control	1	0	0	0	1	0
SBA	Control	1	0	0	0	0	0
SY	Control	0	0	0	0	0	0
SE	Control	0	0	1	0	0	0
UA	Control	2	0	0	0	0	0
ZY	Control	0	0	1	0	1	0
AX	Naïve	-	-	-	-	0	0
AL	Naïve	-	-	-	-	0	0
BN	Naïve	-	-	-	-	0	0
DI	Naïve	-	-	-	-	0	0
HH	Naïve	-	-	-	-	0	0
MI	Naïve	-	-	-	-	0	0
MA	Naïve	-	-	-	-	0	0
MXI	Naïve	-	-	-	-	1	0
OI	Naïve	-	-	-	-	1	0
PL	Naïve	-	-	-	-	0	0